

Abstract. — We studied movement of Dungeness crab *Cancer magister* near Tofino, British Columbia using four methodologies. By the first two methods, beam trawling and trap sampling at specific locations, we inferred that males retreated to deeper water in winter and returned to shallower water in spring. Maturing females tended to move from coastal inlets to the more exposed coast. By the third method, a simultaneous analysis of crab movement and mortality using mark-recovery and fishing-effort data, we showed that dispersal was not extensive. Although insensitive to seasonal movement patterns, results of this analysis suggested a pattern of female movement consistent with that inferred from the beam trawl and trap data. By the fourth method, acoustic tagging, we learned that crab movement rates are inconsistent, having observed both large daily displacements (up to 925 m/day) and days of no discernible movement. The latter two analyses suggested that females tended to move about more than males, with the acoustic tagging results indicating less movement by both sexes during winter. Annual instantaneous total mortality, which is composed predominantly of natural mortality, for tagged sublegal-sized males was estimated at 2.5 (95% CI of 2.3–2.8). This is moderately less than our original natural mortality estimate of 2.9–4.5 and confirms that this original estimate was not grossly aberrant due to the confounding of movement with mortality. We estimated annual instantaneous total female mortality, which is also composed predominantly of natural mortality, to be considerably lower than that of males at 1.3 (95% CI of 0.8–1.8).

Movement, Spatial Distribution, and Mortality of Male and Female Dungeness Crab *Cancer magister* near Tofino, British Columbia

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The Dungeness crab *Cancer magister* is fished commercially from Alaska to central California along the Pacific coast of North America. For at least four decades this highly valued species has undergone dramatic cyclical fluctuations in commercial landings, and coincidentally in population abundance (Methot and Botsford 1982), along the Pacific coast from northern California to Washington. These fluctuations have had undesirable economic consequences (Botsford et al. 1983) and potentially could result in serious biological consequences (Botsford and Wickham 1978, McKelvey et al. 1980). Therefore, there has been considerable research focused on developing an understanding of this phenomenon in recent years (Botsford 1986). Studies of this intriguing problem have been pursued methodically, with competing hypotheses systematically being eliminated (Botsford 1986). However, Methot (1986) points out that our understanding of Dungeness crab population dynamics is still limited by a lack of information on basic population processes such as growth, mortality, movement, and reproduction.

Studies of basic processes serve three purposes. Firstly, new information helps us develop a more complete understanding of complex processes. Inobvious gaps in our understanding of complex processes can cause frustrating failures to explain observed phenomena. Secondly, population

models will be more realistic when supported by confident parameter estimates for key rate variables of processes generally understood. Thirdly, many studies yield data and information for which there are competing explanations, and further research is required to resolve the hypotheses in competition. A relevant example is our estimate of male Dungeness crab mortality (Smith and Jamieson 1989b) for which movement from the study site was an alternate explanation for the disappearance of tagged crabs.

The primary purpose of this paper is to report some recent progress toward understanding the movement and spatial distributions of male and female Dungeness crab. Dungeness crab population dynamics were studied near Tofino, British Columbia, where a productive regional crab fishery has existed for a number of decades. This site has been a focal point for Dungeness crab studies in British Columbia since 1985 (Jamieson and Phillips 1988, Smith and Jamieson 1989a,b,c). In addition to our studies of movement and spatial distributions, we estimated male and female mortality from a simultaneous analysis of movement and mortality of tagged crabs. The experimental design addressed the problem of movement and mortality being confounded, which plagues many studies, by including information on fishing effort.

The four methodologies we employed for assessing Dungeness crab movement yielded information at different scales of resolution. Beam trawling between June 1985 and September 1986 helped us survey the gross distribution and abundance of male and female crabs 125–140 mm carapace width (CW). Trapping helped us assess the distribution and abundance of females greater than 145 mm CW. We previously assessed male abundance and exploitation using trap sampling data in Smith and Jamieson (1989b). From the beam trawl and trapping data sets we were able to infer some seasonal movement patterns, while our model for analyzing mark-recovery data enabled us to estimate proportional transfer rates of crabs among geographical zones within our study site (see Fig. 1), and mortality. Finally, by acoustic tagging and releasing male and female Dungeness crabs during two periods, August–October 1986 and November 1986–February 1987, we were able to monitor the movement tendencies of individual crabs during summer and winter. Together, all four methodologies enabled us to document a coherent description of the spatial distribution and movement patterns of male and female Dungeness crab near Tofino, British Columbia.

Methods

Site description

All beam trawling, trapping, and tagging were conducted within sheltered coastal waters near Tofino, British Columbia. These waters are generally ≈5–15 m depth and well mixed, with an annual seawater temperature range of ≈6–12°C. Substrate varies from sand along the exposed coast to mud near the head of Lemmens Inlet. These coastal waters have sustained a productive Dungeness crab fishery for several decades possibly due to local mudflats providing good substrate for juvenile crab (Armstrong and Gunderson 1985).

The study site is within Canadian Department of Fisheries and Oceans Statistical Area 24. The fishery in Statistical Area 24 accounted for 13 and 20% of the total weight of Dungeness crab landed in British Columbia in 1985 and 1986, respectively. During 1985 and 1986, 27 and 59 vessels, respectively, reported landings from Statistical Area 24. Of the 59 vessels which landed crab in 1986, 30 fished in the study site, and these 30 vessels accounted for approximately 80% of the 265 t landed from Statistical Area 24 in 1986. The fishery near Tofino was exploited year-round and fishing effort was sufficient to capture most males soon after their molt to legal size. Annual instantaneous fishing mortality was estimated at $F = 5.1\text{--}6.9$ (Smith and Jamieson 1989b). No crab fishing occurs in marine waters inland of the study site due to poor crab habitat.

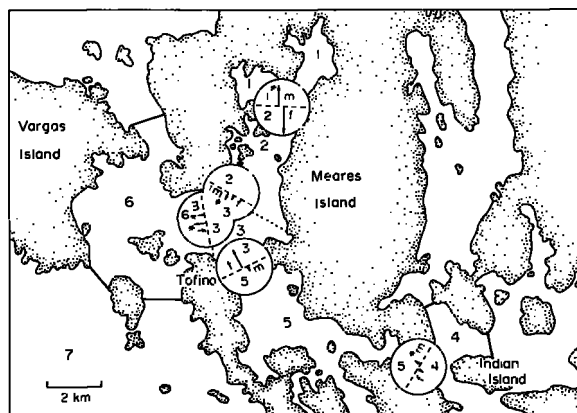


Figure 1

Map of the coastal region near Tofino, British Columbia, demarcating the geographical zones within the study site. Also shown are the relative net movement vectors across boundaries between adjacent zones for both male (m) and female (f) Dungeness crabs. The zone designation is indicated by the numbers both on the map and within the vector circle. These vectors illustrate the net directional tendencies across zone boundaries and their relative magnitude under the assumption of equal crab densities in all zones. An asterisk (*) indicates the vector magnitude is significantly ($P < 0.05$) different from zero. Zones 1–3 are in Lemmens Inlet; zone 5 is Browning Passage.

Beam trawl sampling

In order to assess crab spatial distribution and abundance throughout the study site, we made more than 50 tows with a beam trawl (Gunderson et al. 1985, Gunderson and Ellis 1986) from June until August 1985. In addition, in areas where crabs were abundant and in a few other strategic areas, we made tows at approximately monthly intervals until September 1986. Date, tow depth, bottom type, and area swept were recorded for each tow. Crabs were sexed and their carapace widths measured. We define carapace width (CW) as the distance between the notches just anterior to the tenth anterolateral spines rounded down to the nearest millimeter. Area swept was estimated by multiplying the effective swept width of the beam trawl (2.3 m) by the distance towed. By ranging landmarks at the beginning and end of a tow of 5–10 minutes duration, we were able to calculate distance towed from high-resolution aerial photographs. Most tows were 200–500 m. Our beam trawl was assumed to be efficient and equally selective for crabs up to 135–140 mm CW. We captured very few crabs larger than 140 mm CW by beam trawl. Because it is unlikely a beam trawl captures all crabs in its path, minimum estimates of crab

densities were obtained by dividing the number of crabs captured in a tow by the area swept.

Trap sampling

The abundance of large (>145 mm CW) female crabs was assessed by sampling the catch of commercial fishermen onboard their vessels. The number and carapace width of crabs caught were recorded as were the date and location of the sample. We report two indices of female abundance: $n/\text{trap} \cdot \text{soak day}$ and virtual catch rate (Smith and Jamieson 1989a). Virtual catch rate ($n/\text{trap} \cdot \text{day}$) is the rate at which crabs would enter a trap if initial entry rates were not reduced by changes in bait effectiveness over time and agonistic interactions among crabs.

Fishing effort survey

The number of traps fished by all local fishermen, including the three fishermen who agreed to maintain records of all tagged crabs recovered in the study site, was determined by interviewing fishermen at least monthly from April 1985 until November 1986. The number of traps hauled each month in each of the seven zones demarcated in Figure 1 was estimated by incorporating trap-count data with haul-frequency data. We also maintained a record of the number of our own research trap hauls. We validated our fishing effort survey by comparing the estimated number of traps in Lemmens Inlet each month, as obtained in fishermen interviews, with the number of trap buoys we counted in Lemmens Inlet each month. With few exceptions each trap buoy indicated one trap. Trap buoys were easily counted from a moving boat on calm water in this enclosed body of water. Figure 2a compares the estimated number of traps fished in Lemmens Inlet by each method and indicates that the fishermen's interviews provided an acceptable census of trap abundance.

Mark-recovery

We tagged and released 4038 sublegal-sized male (\bar{x} 142 mm CW, with 95% between 106 and 162 mm CW) and 1246 female (\bar{x} 150 mm CW, with 95% between 135 and 160 mm CW) Dungeness crabs from April 1985 to May 1986. Blue, individually numbered, 4.1-cm T-bar anchor tags (Floy Tag and Manufacturing Company, Seattle, WA) were inserted through the right posterior epimeral suture line, taking care not to puncture internal organs. Crabs to be tagged were obtained from research traps, fishermen, or beam trawls. Before being released, the date, location and tag number were recorded, the crabs were sexed, and their carapace width measured. Release and recovery locations were

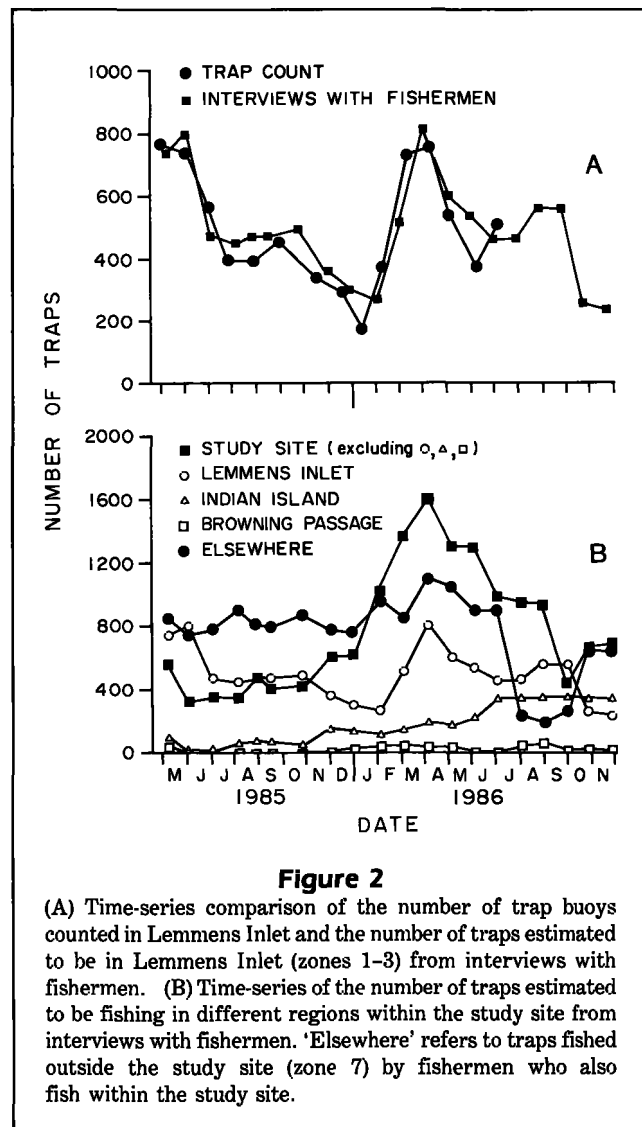


Figure 2

(A) Time-series comparison of the number of trap buoys counted in Lemmens Inlet and the number of traps estimated to be in Lemmens Inlet (zones 1-3) from interviews with fishermen. (B) Time-series of the number of traps estimated to be fishing in different regions within the study site from interviews with fishermen. 'Elsewhere' refers to traps fished outside the study site (zone 7) by fishermen who also fish within the study site.

determined with a grid identification system (0.9×1.2 km) and landmarks.

Most recoveries were obtained from fishermen and research traps. Three fishermen recorded the date, location, and tag number of all tagged crabs they recovered on special recovery forms. Females and sublegal-sized males were returned to the water, but legal-sized males (i.e., >154 mm CW) were generally retained. We asked other fishermen to ignore the recoveries of sublegal-sized crabs, i.e., return them to the water, but to retain tags from legal-sized males. Tags were either given to us or our associates, or we had permission to board a fisherman's vessel at the dock and retrieve tags set aside. From April until August of 1985 and 1986 we saw most fishermen at least biweekly, at other times monthly.

Table 1

Zone area (km²), fishing effort (trap hauls/month), fishing intensity (trap hauls/month · km²), and number of tagged male and female Dungeness crabs released for geographical zones 1–7 (Fig. 1).

Zone	Area	Fishing effort	Fishing intensity	No. of tagged crabs released	
				Male	Female
1	1.23	2234	1734	1438	160
2	0.98	8655	8823	1685	286
3	0.40	16165	40718	537	76
4	0.68	9606	14106	101	95
5	1.31	1053	801	84	11
6	7.56	25294	3345	193	618
7	10 ⁶	15736	0.0157	0	0

Analysis of movement and mortality

We simultaneously analyzed crab movement and mortality using a model structure that facilitated estimation of monthly proportional transfer rates of crabs among the seven geographical zones demarcated in Figure 1. Zone 7 essentially represents the universe outside the study site and provides the option for crabs to vacate the study site. Maximum-likelihood parameter estimates for the transfer rates and mortality were obtained by minimizing the discrepancy between observed and expected number of recoveries in each zone during consecutive one-month intervals of time-at-large. Estimation of expected numbers of recoveries required our fishing-effort survey data. This model

structure allowed us to search for persistent directional movement patterns and obtain male and female mortality estimates that were not confounded by movement of tagged crabs from the study site or into a zone where fishing effort was low.

We organized 920 male and 103 female tag recoveries by the three fishermen and ourselves who recorded all tag-recovery information, and whose fishing effort over time was measured, into frequency cells (O_{ijk}) by zone released ($i = 1, \dots, 7$), zone recovered ($j = 1, \dots, 7$), and months-at-large ($k = 1, \dots, 18$). Therefore, if the observed number of recoveries in cell $O_{4,1,2} = 5$, then 5 crabs released in zone 4 were recovered in zone 1 after 2 months (30–60 days)-at-large. We ignored absolute time, so our analysis was not sensitive to seasonal movement patterns. We also assumed an equal number of trap hauls each month. Although the total number of trap hauls peaks in summer due to an increase in the number of part-time fishermen (Fig. 2b), our assumption is reasonable for the three full-time fishermen, and ourselves, whose tag-recovery and trap-haul data are the only trap-haul data incorporated into this analysis. Monthly fishing intensity (Ricker 1975) for each zone was calculated by dividing the number of trap hauls each month by the area (km²) of the zone (Table 1). Zone 7 was deliberately defined to represent an extremely large area (1 million km²) to ensure that we did not underestimate the rate of movement of tagged crabs from the study site.

The number of tagged crabs initially released in zone i that are present in zone j after k months-at-large (N_{ijk}) is described by the following series of difference Equations (1a–g).

$$N_{i1,k+1} = (N_{i1k}(1 - \Omega_{12}) + \Omega_{21}N_{i2k})s \quad (1a)$$

$$N_{i2,k+1} = (N_{i2k}(1 - \Omega_{21} - \Omega_{23}) + \Omega_{12}N_{i1k} + \Omega_{32}N_{i3k})s \quad (1b)$$

$$N_{i3,k+1} = (N_{i3k}(1 - \Omega_{32} - \Omega_{35} - \Omega_{36}) + \Omega_{23}N_{i2k} + \Omega_{53}N_{i5k} + \Omega_{63}N_{i6k})s \quad (1c)$$

$$N_{i4,k+1} = (N_{i4k}(1 - \Omega_{45}) + \Omega_{54}N_{i5k})s \quad (1d)$$

$$N_{i5,k+1} = (N_{i5k}(1 - \Omega_{53} - \Omega_{54}) + \Omega_{45}N_{i4k} + \Omega_{35}N_{i3k})s \quad (1e)$$

$$N_{i6,k+1} = (N_{i6k}(1 - \Omega_{63} - \Omega_{67}) + \Omega_{36}N_{i3k})s \quad (1f)$$

$$N_{i7,k+1} = (N_{i7k} + \Omega_{67}N_{i6k})s \quad (1g)$$

In these equations, Ω_{ij} represents the proportion of tagged crabs in zone i that move to zone j during any one-month interval. Note that when $i=j$, N_{ij0} is number of tagged crabs released in zone i (Table 1), and that Ω_{ij} 's exist only for adjacent zones (Fig. 1).

The parameter Ω_{76} could not be estimated because no tagged crabs were released in zone 7. The parameter s is monthly survival rate. The annual instantaneous rate of disappearance of tagged crabs (S) is related to s by

$$S = -12 \log_e[s]. \quad (2)$$

Consequent to Equations (1a–g), the expected number of recoveries of tagged crabs released in zone i and recovered in zone j after k months-at-large (E_{ijk}) is

$$E_{ijk} = N_{ijk} q I_j \quad (3)$$

where I_j is monthly fishing intensity (Table 1) in zone j , and q is the catchability coefficient (Ricker 1975).

We employed a multinomial negative log-likelihood function, the separation statistic

$$f_1 = \sum_{ijk} O_{ijk} \log_e [O_{ijk}/E_{ijk}], \text{ for all } O_{ijk} > 0 \quad (4)$$

of Schnute and Fournier (1980), without their factor 2, to evaluate the parameter estimates. In total, the 11 Ω_{ij} 's in Equations (1a–g), q and S required estimation. The model was structured to constrain the Ω_{ij} 's to values between 0 and 1, and to assure the multinomial likelihood condition of

$$\sum_{ijk} O_{ijk} = \sum_{ijk} E_{ijk}. \quad (5)$$

Equation (4) measures the discrepancy between observed (O_{ijk}) and expected (E_{ijk}) frequencies over all frequency cells, and yields maximum-likelihood parameter estimates when f_1 is minimized. We used the SIMPLEX algorithm of Nelder and Mead (1965) as implemented by Mittertreiner and Schnute (1985) to minimize f_1 , while approximate standard errors for the estimates were calculated using the numerical method supplied with Mittertreiner and Schnute (1985). This method uses the matrix of second partial derivatives of f_1 with respect to the parameters (calculated numerically) to generate the asymptotic covariance matrix (Kendall and Stuart 1979). For males we applied the analysis only to recoveries obtained after at least one full month-at-large ($k > 1$), because tagged males were released a short time before fisherman were prepared for the mark-recovery program. Consequently our analysis of male movement and mortality is based on a sample size of 864 recoveries rather than the complete sample of 920 recoveries.

Acoustic tagging

Freshly activated acoustic tags (Smith-Root Inc., Vancouver, WA) were attached longitudinally to the carapace of recently trap-caught hard-shelled male and female Dungeness crabs using fast-drying epoxy. Care was taken to maintain each crab cool and moist while

the carapace was allowed to air-dry for a short period prior to attachment of the tag. Once the epoxy set and we were confident the bond was secure (about one-half hour), each crab was placed in a bucket with fresh seawater to assess its vitality. No crabs appeared to suffer an obvious detriment from the tagging procedure, so all crabs released were anticipated to survive and transmit location information.

Once activated, each 61×14 mm capsule-shaped acoustic tag emits an acoustic signal characterized by a unique transmitting frequency and pulse rate. The bulk of the tag structure is a battery with a transmitting life of ≈ 60 –90 days. With our direction-finding equipment we were able to identify a strong signal up to ≈ 1 km away and subsequently home-in on the location of a tag by audibly or electronically evaluating changes in signal strength. In our study site we were generally able to define the location of a tag to within ≈ 10 –25 m of a chart reference.

During 7–13 August 1986 two male and three female crabs were tagged with acoustic tags, then released near the mouth of Lemmens Inlet (zone 3, Fig. 1). Similarly on 15 November 1986 two male and three female crabs were again tagged and released in the same area. Following the first series of releases we attempted to monitor the location of each crab at least daily, but other commitments, and occasionally being unable to locate the transmitted signal, resulted in the time between observations often exceeding one day. The same limitations applied to the second series of releases, and additionally we only attempted to monitor each crab every three days. All crabs released provided location information for 21–86 days, with the exception of a 140-mm CW male released on 15 November 1986 which was never located after its release.

Mean daily displacement rates for males and females were estimated under the assumption that movement was random from the point of release. We could not entertain a more sophisticated hypothesis with our limited data. Also because of our limited data, we report our results for males and females, and by series (August–October, November–February), with all data from individual crabs combined. Mean daily displacement is the mean expected distance between the location of a crab at the same time on two consecutive days. The maximum-likelihood estimates for mean daily displacement rates (A) were obtained by minimizing the negative log-likelihood function

$$f_2 = \sum_{i=1}^n \{(D_i^2/t_i A) + \log_e[t_i A^2] - \log_e[2D_i]\},$$

for all $D_i > 0$ (6)

where n is the number of observations, and D_i is the linear displacement after t_i days for crab i . When our best measurement for any D_i was zero, we assumed a minimum D_i of 1 m so that Equation (6) was defined for all data points $i = 1, \dots, n$. Our Equation (6) is the maximum-likelihood solution to Equation (3) of Skellam (1951), or Equation (11.6) of Pielou (1977), both of whom develop a mathematical framework for describing random dispersal of individuals from a release point. As for our analysis of movement and mortality, f_2 was minimized and approximate standard errors for A were determined using Mittertreiner and Schnute's (1985) SIMPLEX package.

Results

Beam-trawl and trap sampling

Beam-trawl surveys in 1985 and 1986 captured few Dungeness crabs except in the selected locations considered in the following paragraphs. In 46 beam trawl samples, 2- to 3-year-old (≈ 75 –145 mm CW) male and female crabs (Butler 1961, Stevens and Armstrong 1984, Smith and Jamieson 1989c) were found at densities generally less than 10/hectare (ha). Where much higher densities were found, there were significant seasonal differences, and differences in the relative proportions of males and females. Sampling since 1986 in the same locations (G. Jamieson, unpubl. data) has indicated that the overall abundance of crabs in the 75–145 mm CW size range has dropped to a low level, thus we believe the pattern of spatial and temporal distribution we describe herein is based on observations of essentially one strong year-class.

In upper Lemmens Inlet the densities of male and female 2-year-olds in summer 1985 were initially low and continued to decline throughout 1985 and 1986 (Fig. 3a). This suggests this area is a poor crab habitat since this cohort was abundant elsewhere. The highest density of males was observed in middle Lemmens Inlet (Fig. 3b). During autumn 1985 and the subsequent winter, male densities steadily increased to greater than 1200/ha. Toward the mouth of Lemmens Inlet male densities generally declined (Fig. 3c,d). Because densities of 2-year-old males elsewhere were consistently low, the increase in the number of males in middle Lemmens Inlet is suspected to be due to movement away from exposed shallow water during winter.

We suspect that these males concentrated in middle Lemmens Inlet because of poor habitat further up the inlet. This high density of males eventually decreased rapidly during late spring 1986. Most males were in the normally distributed instar with a mean carapace width of 129 mm and a standard deviation of 12 mm (Smith and Jamieson 1989c), and many molted to legal

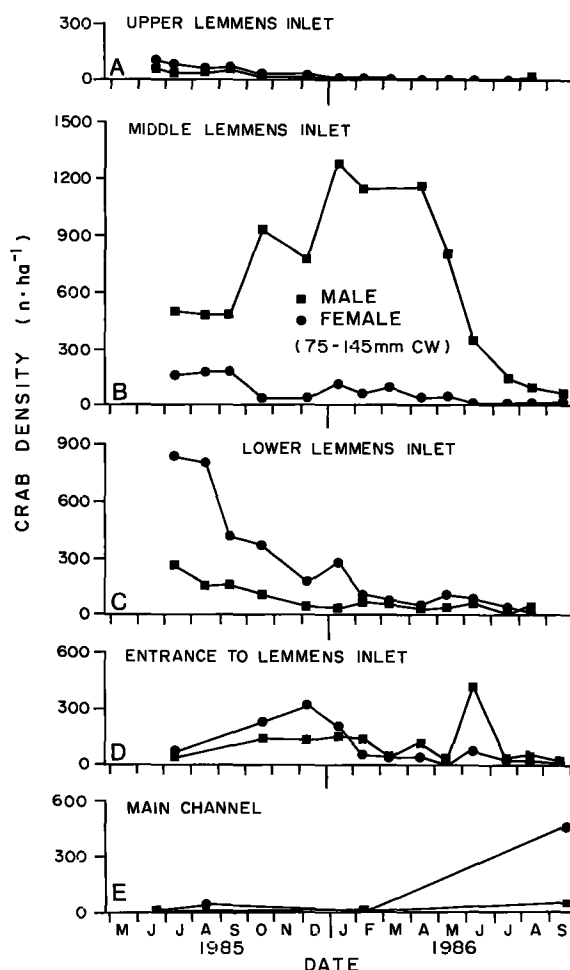


Figure 3

Time-series of densities for 2–3 year-old (≈ 75 –145 mm CW) male and female Dungeness crabs in upper Lemmens Inlet (zone 1), middle Lemmens Inlet (zone 2), lower Lemmens Inlet (zone 2), the entrance to Lemmens Inlet (zone 3), and in the main channel out to sea (zone 6).

size in 1986 (i.e., to the normally distributed instar with a mean carapace width of 156 mm and a standard deviation of 13 mm). Following their molt to legal size they were quickly caught in an intense fishery (Smith and Jamieson 1989b). About 25–35% of the fishing effort in the study site was concentrated in Lemmens Inlet during spring 1986 (Fig. 2b).

A high density of 2-year-old females was observed in the narrow channel at the lower end of Lemmens Inlet in June 1985 (Fig. 3c). Density declined after this date, but increased during autumn in the entrance to Lemmens Inlet (Fig. 3d) 0.5–1.0 km seaward of the narrow channel. Female density further up Lemmens

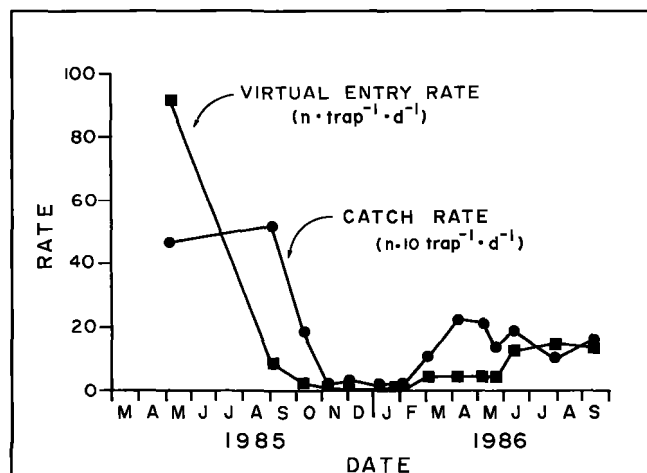


Figure 4

Two indices of abundance for female Dungeness crabs >145 mm CW in zone 6, where females were most abundant (Table 2). The virtual catch rate is the rate at which females would enter a trap if entry rates were not modified by changes in bait effectiveness over time and agonistic interactions among crabs (see Smith and Jamieson 1989a).

Inlet continued to decline, suggesting seaward movement. The increase in female abundance in September 1986 where the main channel out of the study site meets the open coast (Fig. 3e) also suggests seaward movement of females. These females were inferred to be 3-year-olds because they were mainly in the normally distributed instar with a mean carapace width of 137 mm and a standard deviation of 9 mm (Smith and Jamieson 1989c).

The relative abundance of larger females in the study site was assessed by trap sampling. Two indices of abundance obtained from commercial trap samples (Fig. 4), show that females were most readily caught in spring, perhaps because they forage more actively after a winter of incubating eggs. The highest observed abundance of the larger females (>145 mm CW) in spring 1985 and 1986 (Table 2) was in the main channel out of the study site. This is also where (presumably) 3-year-old females in the 137 mm instar were collected in abundance by beam trawl in September 1986. This is consistent with the suggestion from beam-trawl sampling of seaward movement from local inlets as females mature.

Analysis of movement and mortality

Our estimate of the catchability coefficient q for females of 0.198×10^{-5} recoveries per trap haul was about one-seventh that for males (0.138×10^{-4} recov-

Table 2

Abundance ($n/100$ traps · soak day) of female Dungeness crabs >145 mm CW in commercial traps during May and June of 1985 and 1986.

Area samples	Female abundance	
	1985	1986
Upper Lemmens Inlet (zone 1)	7	13
Lemmens Inlet (zones 2 and 3)	15	8
Browning Passage (zone 5)	22	4
Near Indian Island (zone 4)	10	36
Main channel (zone 6)	429	138

Table 3

Maximum-likelihood estimates and standard errors (SE) of the proportion (Ω_{ij}) of tagged male and female Dungeness crabs in zone i transferring to an adjacent zone j during a one-month interval. Asterisks indicate transfer proportions significantly ($P < 0.05$) greater than zero.

Parameter	Male		Female	
	Proportion	SE	Proportion	SE
Ω_{12}	0.15*	0.02	0.84*	0.25
Ω_{21}	0.50*	0.09	0.68*	0.13
Ω_{23}	0.22*	0.02	0.10*	0.03
Ω_{32}	0.16*	0.03	0.07	0.07
Ω_{35}	0.44*	0.06	0.22	0.12
Ω_{53}	0.11*	0.02	0.36	0.27
Ω_{36}	0.40*	0.04	0.63*	0.12
Ω_{63}	<0.01	<0.01	<0.01	<0.01
Ω_{45}	0.12*	0.03	0.01	0.01
Ω_{54}	<0.01*	<0.01	0.09	0.08
Ω_{67}	0.04*	0.01	0.02	0.01

eries per trap haul), indicating males were much more readily caught than females by commercial traps. This difference is mainly due to commercial traps being more efficient at retaining larger crabs which are predominantly males. Consequently it is apparent in Table 3 that our transfer proportion estimates for females are much less confidently made than those for males because of the much smaller number of tagged females recovered.

The proportional transfer rates for males do not suggest any persistent directional movement. We note that there is little transfer of crabs between Indian Island (zone 4) and Browning Passage (zone 5) when compared with the apparent mixing among zones 1, 2, 3, 5, and 6, so the movement of tagged crabs through the deeper water between Browning Passage and Indian Island appears limited. Male crabs appear to vacate middle and lower Lemmens Inlet (zones 2 and 3) at proportional rates of about 0.22 and 0.40 per month with

only a small proportion per month (0.01) entering Lemmens Inlet from zone 6. The monthly proportional transfer rate of crabs from zone 2 to zone 1 (Ω_{21}) of 0.50 seems high compared with transfer of crabs from zone 1 to zone 2 (Ω_{12}) of 0.15, but this might be explained by zone 1 (upper Lemmens Inlet) being poor crab habitat and the possibility that only a small proportion of male crabs are successful in escaping this habitat.

The proportional transfer rates for females have large standard errors and must be interpreted cautiously. However, a notable result is the 0.63 proportional transfer rate for Ω_{36} compared with <0.01 for Ω_{63} , thus indicating that a greater proportion of tagged females vacated lower Lemmens Inlet than entered Lemmens Inlet. The monthly proportional transfer rate of 0.84 for females escaping the poor habitat in zone 1 (Ω_{12}) is high compared with males, but might indicate females are more capable of recognizing the environmental clues leading to more suitable substrate. The transfer rates of females in both directions between zone 1 and zone 2 are notably higher than the male transfer rates, and since the largest release of tagged male and female crabs was in zones 1 and 2, this result might indicate females are generally more mobile than males.

Proportional transfer rates alone are an incomplete interpretation of movement trends, since the zones differ in area and therefore also in crab abundance. Consequently, the high transfer rate for Ω_{36} when compared with Ω_{63} is in large part a result of zone 6 having an area of 7.56 km², whereas zone 3 has an area of 0.40 km². Relative movement vectors were therefore calculated from the transfer-rate estimates under the assumption that crab densities were equal for all zones. For example, if crab density is Δ crabs per km², then the estimated number of crabs transferring from zone 6 to zone 3 in a one-month period is $7.56\Delta\Omega_{63}$.

Figure 1 diagrams net movement tendencies, under the assumption of equal crab densities in all zones, across those zone boundaries where transfer rates in both directions were estimated. Two notable features for males are the strong indication of net movement of males into upper Lemmens Inlet, and a tendency for males to vacate lower Lemmens Inlet and the waters near Indian Island. As previously mentioned, the net movement into upper Lemmens Inlet might be a result of a low proportion of males escaping this poor habitat. It might also indicate dispersion from zone 2 where many males were tagged and released in spring 1986. A large number of males 125–140 mm CW were tagged in zone 2 in spring 1986 because they occurred in high density ($>1200/\text{ha}$) and were readily captured by beam trawl. Beam trawling indicated these crabs apparent-

Table 4

Maximum-likelihood estimates and standard errors (SE) of mean daily displacements (A , m/d) of male and female Dungeness crabs.

	Male			Female		
	<i>n</i>	Estimate	SE	<i>n</i>	Estimate	SE
Aug 86–Oct 86	31	321	29	30	500	45
Nov 86–Feb 87	8	74	13	15	161	21
Combined	39	288	23	45	419	31

ly dispersed, or molted to legal size and were caught, by summer 1986 (see previous section). For females there is a general, although non-significant, tendency to vacate Lemmens Inlet and Browning Passage. This result is consistent with our beam-trawl and trapping results (previous section) which also demonstrate a net seaward movement of females from Lemmens Inlet.

We estimated the annual rate of disappearance of tagged crabs with reasonable confidence at $S = 2.54$ (SE 0.13) and $S = 1.28$ (SE 0.27) for males and females, respectively. Corroborating these high estimates for S , our analysis estimated that only about 2% and 7% of tagged males and females, respectively, left zones 1–6, i.e., moved to zone 7, over the time-period of our study. In other words, the distribution over time of tag recoveries in zones 1–6 could not be well explained by a high transfer rate into zone 7 where crabs might not be recovered due to a low fishing intensity. Thus these estimates for S were obtained despite our model structure providing an exaggerated opportunity for crabs to disperse to zone 7 as an alternative explanation for the disappearance of tagged crabs, i.e., as an alternative to mortality. This conclusion appears to validate our original assumption that few tagged crabs left our study site during the study period (Smith and Jamieson 1989b).

Based on a double-tagging study, Smith and Jamieson (1989b) concluded that tag loss by sublegal-sized crabs is low and therefore unlikely to be an important source of tag disappearance. Observations of tank-held crabs over several months did not reveal differential mortality of tag and untagged crabs. Thus we conclude that the values for S estimated in this study represent mainly natural mortality and, in the case of males, tag disappearance due to molting to legal size with subsequent exploitation. However, because only about 5% of tagged sublegal-sized males were reported caught as legal-sized crabs (210 recovered when legal-sized of the 4038 released when sublegal-sized), despite high fishing mortality ($F = 5.1$ – 6.9) and apparently good compliance in reporting recovered tags ($\approx 87\%$), we con-

clude that our male estimate for *S* measures mainly natural mortality of sublegal-sized males. We recognize, however, that there is likely some degree of mortality due to trapping and handling by fishermen. Similarly, and in consideration that females are not commercially fished, we are confident that our female estimate for *S* also mainly measures natural mortality.

Acoustic tagging

From the means and standard errors of the movement rate estimates (Table 4) we conclude that for both the August and November 1986 releases of acoustically tagged crabs, females tended to move about significantly ($P < 0.01$) more than males. Similarly, during August–October 1986 both males and females seemed to move at rates about 3 to 4 times faster ($P < 0.01$) than those for November 1986–February 1987. We realize, however, that our male results for the latter time period are based on observations of just one crab. Slower movement during winter for both male and female crab is consistent with the poikilothermic habit of marine invertebrates in that respiratory activity is closely related to temperature. Our analysis of movement based on the mark-recovery data also hints that females are more mobile than males.

We cannot conclude that our estimate of a faster movement rate for females, relative to males, represents a general phenomenon for all Dungeness crab populations. Our acoustic tagging results are possibly peculiar to our study site, since the greater movement rate for females is consistent with our interpretation of the trapping and beam trawl results which suggest that females tend to vacate the coastal inlets in search of the exposed coast. Further, we caution that our dispersal rate estimates for males and females from the acoustic tagging data should be considered minimum estimates because the archipelago in which the acoustically tagged crabs were released will tend to restrict the potential for movement. Also, our assumption of random dispersal from the point of release of an acoustically tagged crab is probably too strict. Our beam trawl and trapping data indicate that both males and females might move in response to environmental clues such as tides and currents; and our beam-trawl, trapping, and mark-recovery data all suggest seaward movement of females from Lemmens Inlet.

These limitations to our interpretation of the acoustic tagging data preclude us from obtaining precise rates of population dispersal over time. However, we think that there is some value in presenting approximate dispersal rates since they can be compared with the results of our analysis of movement and mortality, and to some degree with Dungeness crab movement rates that might be obtained from other regions. Conse-

quently, the mean daily displacement rates (*A*) of 288 m/day and 419 m/day obtained for males and females, respectively, suggest that after one year of random dispersal, in the absence of geographical boundaries, 95% of males and females would be within radii of 9.5 and 13.9 km, respectively, of the point where they were one year previous. These radii were determined from

$$r^2 = -\log_e[p_{rt}]A^2t \quad (7)$$

where *r* is the radius within which the proportion $1 - p_{rt}$ of a randomly dispersing population is expected after *t* days (Pielou 1977). These estimates of *r* agree favorably with the results of our simultaneous analysis of movement and mortality from our mark-recovery data in that about 2% and 7% of male and female crabs, respectively, were estimated to leave the study site during the 18-month study period. The study site encompasses an area of about 5–10 km radius around Tofino (Fig. 1).

Discussion

The four methodologies we employed to assess male and female Dungeness crab movement provided insights at different levels of resolution and from different perspectives. The methodologies were complementary and together allowed us to document a coherent description of Dungeness crab movement near Tofino, British Columbia. For example, acoustic tagging gave us a general indication of the dispersal rates for individual male and female crabs (summer and winter) which was consistent with the results of our simultaneous analysis of movement and mortality using mark-recovery data. The former analysis suggested that the dispersal rates would maintain 95% of the male and female populations within about 10 km and 14 km, respectively, of points of release, while the latter analysis suggested that only about 2% of males and 7% of females would escape the study site (about 10–15 km radius) during our 18-month study period. In addition, both the beam-trawl and trap samples documented seasonal changes in the relative distributions and abundances of males and females which could not be gleaned from the acoustic tagging and mark-recovery data alone.

Overall, our four sources of movement information suggest that male Dungeness crab undergo only limited movements within the local archipelago. There was no evidence of migratory movement, but males were inferred to move to shallower water (≈ 10 m) during summer, then to retreat to more sheltered habitat in autumn. Others have observed, or inferred, similar behavior for this species. Stevens and Armstrong (1984)

reported that juvenile males and females of the 1980 year-class in Grays Harbor, Washington, disappeared during the winter of their first year, then reappeared the following spring. Gotshall (1978) observed movement of sublegal- and legal-sized male crabs in northern California to deeper water in winter, and a return to shallower water in spring. It is reasonable to surmise that the autumn movement to deeper water is to avoid rough shallow water during the winter. Returning to shallower, warmer, and more productive water during summer could enhance growth and survivorship.

Our estimated average daily displacement rate for male Dungeness crabs of ≈ 300 m/day, is consistent with our inferences on movement from our mark-recovery, beam-trawl, and trap sampling results. Our general conclusion of limited movement is also consistent with the results of other tagging studies. Both Butler (1957) for Dixon Entrance, British Columbia, and Gotshall (1978) for northern California, suggested that Dungeness crab populations remain local. With the exception of the apparent seasonal shift in habitat, no studies suggest migratory movements for males; however, Gotshall (1978) noted that males seem to move in the direction of prevailing currents off northern California. Bennett and Brown (1983) report that most tagged males of the closely related crab *Cancer pagurus* remained near where they were released in the English Channel.

Our acoustic tagging and mark-recovery data suggest that female Dungeness crab undergo only limited movement. Diamond and Hankin (1985) similarly argued that mature female Dungeness crab off the coast of northern California undergo limited movements and suggested that females constitute localized stocks. Diamond and Hankin (1985) do suspect that females move short distances to shallower water in spring to mate and molt. Our analyses provided no evidence of this, but it is quite conceivable that both males and females could improve mating opportunities by concentrating in shallow water (Butler 1960).

We inferred, mainly from our beam trawl and trap samples, that females tended to move from coastal inlets to an area more exposed to the open coast (zone 6, Fig. 1). In the inlets the substrate ranged from mud to a mud/sand mix, whereas in the more exposed area the bottom was mainly sand or a sand/gravel mix. Wild (1980) states that females must be at least partially buried in sandy substrate to extrude and incubate eggs so our inference is consistent with the current understanding of the life history of Dungeness crab females. Stevens and Armstrong (1984) noted that egg-bearing females were rare in Grays Harbor, and speculated that most mature females left the harbor to incubate and release their eggs in a preferred environment. Our study yielded an average daily displacement rate for

females (≈ 400 m/day) which was significantly ($P < 0.01$) more than the rate for males (≈ 300 m/day), and which might be explained by females undergoing deliberate migratory movements to locate suitable substrate for incubating eggs.

Similar movement behavior has been reported for females of other crab species. Hyland et al. (1984) observed the movement of female portunid crab *Scylla serrata* from an estuarine environment, where they lived as juveniles, to the open ocean where they released their eggs. Some females returned to inshore waters after the hatching season. Bennett and Brown (1983) demonstrated that female *C. pagurus* undergo extensive movements, apparently to locate habitat more suitable for egg incubation and release. While SCUBA diving, Howard (1982) observed egg-bearing female *C. pagurus* congregated in relatively deep (24 m), quiet water. Since they were rare elsewhere, he concluded this was a preferred habitat. Dinnel et al. (1987) observed a similar behavior for Dungeness crab in Puget Sound, Washington, from the Government of Canada submersible *Pisces IV*.

Our simultaneous analysis of Dungeness crab movement and mortality using mark-recovery and fishing-effort data diminished the confounding of these two processes and yielded a revised estimate of the natural mortality rate originally proposed by Smith and Jamieson (1989b). Our (mainly) natural mortality rate estimate for males of 2.5 (95% CI of 2.3–2.8) is moderately lower than our previous estimate of 2.9–4.5, probably because of dispersal of tagged crabs into zones (especially zone 6) with low fishing intensities.

Our estimate of female natural mortality of 1.3 (95% CI of 0.8–1.8) is significantly lower than that of males but in general agreement with the mortality estimates of Hankin et al. (1985, 1989) for females in northern California. They estimated annual instantaneous natural mortality for females greater than 140 mm CW at 2.0 and 2.5 for two different periods of release in a mark-recovery experiment. For females 125–140 mm CW their rough estimate was ≈ 0.7 , a more precise estimate being unobtainable due to females this size having a high probability of molting and changing vulnerability to traps. Our estimate of 1.3 is based on a group of tagged females whose carapace widths at release were 135–171 mm (\bar{x} 150 mm), thus our estimate seems consistent with those of Hankin et al. (1985, 1989).

The estimates of male and female natural mortality from this study, and of female natural mortality from Hankin et al. (1985, 1989), for crabs near the Canadian minimum legal size limit of 154 mm CW (165 mm spine-to-spine CW) increases our confidence that mortality of mature Dungeness crab is indeed high. For example, a mortality rate of 2.0 means only 13.5% annual

survivorship. The recognition of such a high mortality rate for adults of this commercially important species immediately prompts questions regarding the appropriateness of both the Canadian and American (≈ 159 mm CW) minimum legal carapace width limits for optimizing two of the most basic stock-management guidelines: yield-per-recruit and eggs-per-recruit.

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